Anterior Intraparietal Sulcus is Sensitive to Bottom–Up Attention Driven by Stimulus Salience

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Abstract

■ Frontal eye fields (FEF) and anterior intraparietal sulcus (aIPS) are involved in the control of voluntary attention in humans, but their functional differences remain poorly understood. We examined the activity in these brain regions as a function of task-irrelevant changes in target and nontarget perceptual salience during a sustained spatial attention task. Both aIPS and FEF were engaged during selective attention. FEF, but not aIPS, was sensitive to the direction of spatial attention. Conversely, aIPS, but not FEF, was modulated by the relative perceptual salience of the target and nontarget stimuli. These results demonstrate separable roles for FEF and aIPS in attentional control with FEF more involved in goal-directed spatial attention and aIPS relatively more sensitive to bottom–up attentional influences driven by stimulus salience. ■

INTRODUCTION

The ability to filter out distracting visual information is critical for successful performance of an individual's goals. For example, it is vital to pay attention to the road when driving despite the fact that an accident has occurred on the side, but it is also necessary to maintain a certain level of unfocused vigilance in case an unexpected, but behaviorally relevant, event occurs, such as a car suddenly merging into your lane. The tension between maintaining voluntary attention on task-relevant objects and automatic orienting toward perceptually salient, but currently task-irrelevant, events has a long history within the psychological literature (e.g., Proulx & Egeth, 2006b; Berger, Henik, & Rafal, 2005; Geng & Behrmann, 2005; Kristjansson, Wang, & Nakayama, 2002; Yantis & Egeth, 1999; Lavie, 1995; Theeuwes, 1995; Muller & Rabbitt, 1989; Nakayama & Mackeben, 1989; Jonides & Yantis, 1988; Gibson, 1986; Eriksen & Yeh, 1985; James, 1890/1983; Jonides & Irwin, 1981; Posner, Snyder, & Davidson, 1980). These studies report costs in task-related behavioral outcomes (e.g., lower accuracy and/or slower reaction times) when nontargets have greater perceptual salience and/or similarity with the target. Although there is disagreement regarding whether completely task-irrelevant stimuli can capture attention or not (e.g., Leblanc, Prime, & Jolicoeur, 2008; Hickey, McDonald, & Theeuwes, 2006), there is good agreement that behavioral decrements in target discrimination reflect nontarget competition for target-related attentional processing, which lead to attentional capture by the nontarget.

The neural system for controlling voluntary visual attention in humans is well known to include the frontal eye fields (FEF) and areas in the parietal cortex, particularly the intraparietal sulcus (IPS) and the superior parietal lobule (SPL) (e.g., Kelley, Serences, Giesbrecht, & Yantis, 2007; Serences & Yantis, 2007; Slagter et al., 2007; Sylvester, Shulman, Jack, & Corbetta, 2007; Geng et al., 2006; Shomstein & Behrmann, 2006; Kincade, Abrams, Astafiev, Shulman, & Corbetta, 2005; Kristjansson, Vuilleumier, Malhotra, Husain, & Driver, 2005; Behrmann, Geng, & Shomstein, 2004; Corbetta & Shulman, 2002; Yantis et al., 2002; Driver & Frackowiak, 2001; Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Hopf et al., 2000; Hopfinger, Buonocore, & Mangun, 2000; Nobre, Gitelman, Dias, & Mesulam, 2000; Gitelman et al., 1999; Paus, 1996). These areas have been characterized as attentional "control" regions that bias responses in the sensory cortex (e.g., by increasing response gain) associated with the attended location or feature (see also Bestmann, Ruff, Blakemore, Driver, & Thilo, 2007; Liu, Larsson, & Carrasco, 2007; Serences & Boynton, 2007; McMains & Somers, 2004; Hopfinger et al., 2000; Kastner & Ungerleider, 2000; Brefczynski & DeYoe, 1999; Gandhi, Heeger, & Boynton, 1999; Luck, Chelazzi, Hillyard, & Desimone, 1997; Chelazzi et al., 1995); Mircrostimulation and transcranial magnetic stimulation of FEF and the parietal cortex in monkeys and humans have shown direct modulation of activity in the retinotopic visual cortex, which results in increased perceptual sensitivity to stimuli

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in corresponding locations of the visual field (e.g., Ruff et al., 2006, 2008; Armstrong, Fitzgerald, & Moore, 2006; Chambers, Stokes, Janko, & Mattingley, 2006; Mevorach, Humphreys, & Shalev, 2006; Muggleton et al., 2006; Silvanto, Lavie, & Walsh, 2006; Hung, Driver, & Walsh, 2005; O'Shea, Muggleton, Cowey, & Walsh, 2004; Moore & Armstrong, 2003; Grosbras & Paus, 2002). These studies suggest that frontal and parietal areas contain representations of attentional priority that selectively enhance processing in the sensory cortex of the related stimulus or feature. Such attentional enhancement of the sensory cortex leads in turn to better behavioral performance as indexed by faster detections and more accurate discriminations.

In comparison to studies of voluntary attentional selection, there have been relatively few studies examining the representation of sensory-driven attentional processes. These studies frequently employed spatial cues that either incorrectly predicted the location of an upcoming target stimulus or captured attention automatically (e.g., Posner et al., 1980). For invalid spatial cues, effects of sensory-based attentional reorienting toward the target have been reported in the temporal–parietal junction (TPJ) near the intersection of the angular gyrus and the superior temporal lobe (Corbetta, Patel, & Shulman, 2008; He et al., 2007; Indovina & Macaluso, 2007; Astafiev, Shulman, & Corbetta, 2006; Vossel, Thiel, & Fink, 2006; Kincade et al., 2005; Thiel, Zilles, & Fink, 2004; Mort et al., 2003; Corbetta & Shulman, 2002; Downar, Crawley, Mikulis, & Davis, 2000; Friedrich, Egly, Rafal, & Beck, 1998). Importantly, under conditions of invalid spatial cues, sensory-driven attentional reorienting was always in response to violations in task-related expectancies. In the case of exogenous spatial cues that automatically capture attention, more mixed results have been reported. Some studies have also found exogenous cues to activate the inferior parietal lobe in or within the vicinity of TPJ (Mayer, Dorflinger, Rao, & Seidenberg, 2004; Peelen, Heslenfeld, & Theeuwes, 2004; Mort et al., 2003; Corbetta et al., 2000; Rosen et al., 1999), but others have also reported overlap with structures involved in voluntary attentional tasks such as FEF and the superior parietal cortex (e.g., Kincade et al., 2005; Mayer, Dorflinger, et al., 2004; Mayer, Seidenberg, Dorflinger, & Rao, 2004; Peelen et al., 2004; Kim et al., 1999; Rosen et al., 1999). Among these studies however, it was not always clear whether areas were driven specifically by the exogenous cue or also by the appearance of the target. When the exogenous cue was dissociated from the appearance of the target, the overlap with areas involved in voluntary attention was considerably less (e.g., Kincade et al., 2005).

In addition to studies with a spatial cue, sensory-driven attentional processes have also been examined by manipulating target and nontarget similarity. For example, Serences and Yantis (2007) examined the effects of "contingent" attentional capture by nontargets that share the target's color (and therefore the sub-jects' attentional control settings). Greater activation was found in contralateral IPS and FEF in response to target-colored nontargets compared to non-target-colored nontargets, demonstrating that target-colored nontargets were more likely to capture attention and have higher attentional priority (Serences & Yantis, 2007; Mevorach et al., 2006; Serences et al., 2005). The idea that frontal and parietal areas operate as an attentional "salience" or "priority" maps (e.g., Gottlieb, 2007; Itti & Koch, 2000) that code the behavioral relevance and perceptual salience of objects has also been suggested by results from single-cell recording studies in monkey FEF (e.g., Balan & Gottlieb, 2006; Bichot & Schall, 2002) and the lateral intraparietal sulcus (LIP; Bisley & Goldberg, 2006; Goldberg, Bisley, Powell, & Gottlieb, 2006; Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006; Kusunoki, Gottlieb, & Goldberg, 2000; Platt & Glimcher, 1999; Thompson, Bichot, & Schall, 1997). Here, the degree to which a stimulus drove neuronal firing was determined by goal-directed attributes such as being the target but also by perceptual qualities such as luminance or contrast. Similar to many human studies, however, the sensory-driven properties were also often related to the target (e.g., by being a potential target in a visual search display, or by predicting the location of an upcoming target).

Taken together, these previous studies suggest that FEF and IPS may not be strictly a "voluntary" attentional system, but rather reflect the integration of attentional priority for various objects in the visual field. In this study, we explored the degree to which FEF and IPS each represent sensory-driven attentional orienting. We used a sustained spatial attention task in which the location of the target was blocked and known in advance of each target appearance. Subjects were explicitly cued with 100% validity to attend to one of two "mask" stimuli located in the lower left and right visual fields so that there was no ambiguity regarding the location to which spatial attention should be directed. Perceptual salience was manipulated by luminance and contrast (Proulx & Egeth, 2006a; Carrasco, Ling, & Read, 2004; Reynolds & Desimone, 2003; Bundesen, 1990), and was randomly assigned to be a feature of the attended or unattended object, or be absent.

Importantly, perceptual salience was irrelevant to target detection, discrimination, or response and, therefore, any attentional capture by a salient stimulus (and particularly a salient nontarget) can be understood as being sensory-driven and not dependent on target-related attentional control settings. The location of the target and the required discrimination task was completely orthogonal to the feature of perceptual salience and this design constituted a conservative test of sensory-driven attentional processing. We additionally included a control condition in which the same stimuli were presented under conditions of passive viewing, which controlled for visual effects when no attention was required.

To anticipate our results, we found that both the anterior IPS (aIPS) and FEF were engaged during selective attention, but that FEF was additionally sensitive to the direction of goal-directed spatial attention. Conversely, aIPS integrated voluntary and sensory-driven attention such that activation was greatest for salient nontargets. aIPS activation also correlated strongest with RT when the nontarget was salient. These results demonstrate separable roles for FEF and aIPS in attentional control, with FEF more involved in goal-directed spatial attention and aIPS integrating information about the perceptual saliency of visual inputs during attention.

METHODS

Subjects

Fifteen volunteers (6 women, 15 right-handed), ranging in age from 18 to 34 years in age, participated. All were screened for MRI compatibility and gave written informed consent in accord with the local ethics clearance as approved by NIH. All had normal or corrected-to-normal vision. Data from three subjects were excluded because they failed to perform the task to criterion (70% accuracy).
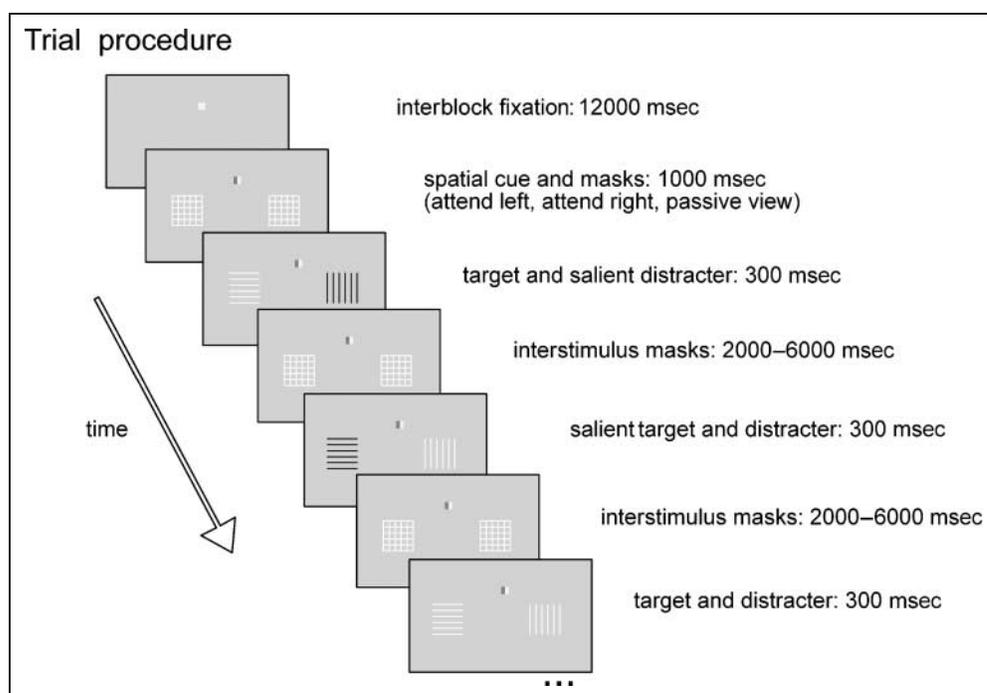
Experimental Design

The experiment had a 3 × 3 factorial design. The factors were location of cued spatial attention (left, right, passive) and location of a perceptually salient stimulus (left, right, absent). Spatial attention was mini-blocked in groups of six trials. Within each block, salience was pseudorandomly selected for each trial, with the constraint that each block contained two samples from each salience condition. Each block lasted 24 sec and was followed by a 12-sec period of blank fixation. Each of the three attention blocks occurred in a random order within a meta-block that included one sample of each spatial attention condition and three blank fixation periods. Four meta-blocks were included in each of five sessions.

A central fixation square that subtended 0.14° visual angle, was continuously displayed, but changed (see Figure 1) at the beginning of each block to indicate which attentional set (attend left, attend right, or passively fixate) should be maintained for the following block of trials. Each block began with the appearance of the attentional cue and bilateral ''mask'' stimuli for 1000 msec to permit establishment of an attentional set (Figure 1). The two ''masks'' were white (75.8 cd/m^2), and the background was gray (51.0 cd/m^2; Michelson contrast value = 0.20). The nearest corner subtended 1.26° and 0.28° of horizontal and vertical visual angle from central fixation and the furthest corners subtended 2.23° and 1.25°, respectively.

Each trial then consisted of a simultaneous change in both ''mask'' stimuli from square grids to vertical or horizontal lines. The vertical and horizontal lines were components of the original checked ''mask'' stimulus and therefore produced no visual onset. Whether the lines were vertical or horizontal was randomly and independently determined for each stimulus on each trial. Nonsalient stimuli were identical in color and luminance (see above) to the original masks, whereas salient stimuli were black and had higher contrast than the ''masks'' from the background color (3.51 cd/m^2; Michelson contrast value = 0.87). We wanted to avoid

Figure 1. Illustration of possible trial sequence during a block of attention to the left. Each stimulus block began with a period of blank fixation followed by the onset of bilateral mask-stimuli and a fixation square that cued attention to the left or right, or indicated passive viewing (note stimuli are not drawn to scale for illustrative clarity). On each trial, the masks changed into vertical or horizontal lines that remained visible for 300 msec. On some trials, either the target or the nontarget was perceptually salient, as defined by a change in color and contrast. A variable delay followed each trial during which subjects responded with a manual button press to indicate the perceived orientation of lines on the attended side.

Trial procedure

interblock fixation: 12000 msec

spatial cue and masks: 1000 msec
(attend left, attend right, passive view)

target and salient distracter: 300 msec

interstimulus masks: 2000–6000 msec

salient target and distracter: 300 msec

interstimulus masks: 2000–6000 msec

target and distracter: 300 msec

time

using visual onsets to capture attention and therefore chose a change in color and luminance to define perceptual ''salience,'' a method known to capture attention (e.g., Carrasco, 2006; Proulx & Egeth, 2006a; Carrasco et al., 2004; Reynolds & Desimone, 2003; Bundesen, 1990). The target and nontarget were visible for 300 msec after which the ''mask'' gratings reappeared (Figure 1).

The average intertrial interval varied between 2 and 6 sec to allow for uniform sampling of event-related BOLD responses across the whole TR and to maintain behavioral uncertainty regarding the onset of the next target stimulus. Subjects were instructed to indicate via right-handed button press using an MRI-compatible response box whether the stimulus on the attended side was composed of vertical or horizontal lines. Mapping of response choice to the index or middle finger was counterbalanced across subjects. Behavioral training was conducted outside the scanner until the participant understood the task and demonstrated the ability to perform correctly. All subjects were instructed to maintain visual fixation throughout the experiment and their eye position was monitored throughout the experiment (see below). Stimuli were presented via a video projector and front projection screen. The screen was viewed via a mirror system attached to the head coil.

Eye Tracking

Eye tracking was performed at 60 Hz using Applied Science Laboratories (ASL, Bedford, MA) model 504 with long-range remote optics. Data were acquired from 10 out of 12 subjects; two subjects could not be adequately tracked. For analysis, eye position data were filtered by removing a linear trend and values exceeding approximately twice the distance of the furthest edge of the stimulus, which could be caused by artifacts unrelated to the experimental manipulation such as blinks, or loss of data. The data were then smoothed with a 5-point moving average to remove remaining noise artifacts.

Image and Data Processing

MRI data were acquired from a 3-T Siemens Trio scanner (Siemens, Erlangen, Germany) equipped with an eight-channel phased array head coil. A T2*-weighted echo-planar imaging (EPI) sequence was used to acquire volumes of 34 slices of 3 mm thickness (3 × 3 mm in-plane resolution) with a distance factor of 10%, every 2000 msec. Slices were axially oriented and covered the whole brain. Two hundred twenty-two volumes were collected in each session of five sessions. Image data were analyzed using SPM5 (Wellcome Department of Imaging Neuroscience, London, UK; Friston et al., 1995). Prior to statistical analysis, the first four volumes

were discarded to allow for T1 equilibrium effects. Images were realigned and unwarped to correct for interactions between movement and field inhomogeneities (Andersson, Hutton, Ashburner, Turner, & Friston, 2001); normalized to the MNI EPI template available in SPM 5, and resampled to a resolution of 2 × 2 × 2 mm. Data used in group image analyses were additionally smoothed with a three-dimensional 6-mm FWHM Gaussian kernel. Region-of-interest (ROI) data extracted from each participant separately were not spatially smoothed.

High-resolution (1 × 1 × 1) T1-weighted structural images were acquired using an MP-RAGE sequence, co-registered with each subject's EPI images, and normalized to the MNI template brain. These were used for identifying individual anatomical landmarks for ROI selection (see below). An average structural image was created from the normalized T1-weighted images for the purpose of displaying functional results from the group.

Experimental factors were first modeled for each subject by a stick function convolved with a canonical hemodynamic response function. Linear contrasts of parameter estimates were estimated for each subject and combined for the group level in random effects general linear model. Results from the group level were used to guide individual ROI selection (see below). Behavioral data and image data extracted from individual ROIs were analyzed using R software (www.r-project.org).

Regions of Interest Identification in Individuals

Six ROIs corresponding to human FEF, aIPS, and dorsal middle occipital gyrus (dMOG) bilaterally were extracted from each subject. In contrast to data used for group analysis, data extracted from individual ROIs were not additionally spatially smoothed after realignment and normalization. Selection of ROIs was accomplished by using results from group random effects analyses to guide selection of the functional peak in each individual nearest to anatomical landmarks. Using general task constraints combined with anatomical criteria provided individual specificity while still maintaining the advantages group statistics that permit generalization to the population (Ikkai & Curtis, 2007; Stephan, Marshall, Penny, Friston, & Fink, 2007).

For aIPS and FEF, coordinates from the group random effects analyses were based on the contrast of attention minus passive viewing, ($p < .0001$, cluster size ≥10 voxels; Table 1) and those for the left and right dMOG were based on contrasts between contralateral and ipsilateral attention to isolate regions with visual representations corresponding to the lower left and right visual field, ($p < .001$, cluster size ≥10 voxels; Table 1). Data from one hemisphere could not be reliably extracted for two subjects in dMOG and data from those subjects were not included in ROI analyses.

The ROI-defining contrasts were orthogonal to any comparisons involving the salience conditions, which

Table 1. Significant Cortical and Subcortical Regions from Whole-brain Group Analysis

Cluster Size	t Score	Z Score	x y z mm	Region Name
Attention Left + Right > Passive Viewing				
465	8.94	4.73	−28 −48 44	L intraparietal sulcus
	13.98	5.58	−40 −40 46	
	5.52		−20 −66 46	L posterior intraparietal sulcus
12	6.18	3.98	32 −50 44	R intraparietal sulcus
18	7.38	4.35	44 −36 46	R intraparietal sulcus
334	11.17	5.16	−36 −4 50	L posterior middle frontal gyrus (frontal eye fields)
39	6.15	3.97	32 −4 48	R posterior middle frontal gyrus (frontal eye fields)
392	9.86	4.92	−4 4 52	L + R medial frontal gyrus
44	8.13	4.54	−60 8 26	L inferior frontal gyrus
1250	14.25	5.62	−24 12 4	L putamen
502	11.01	5.14	22 10 4	R putamen
52	8.55	4.64	−32 −34 74	L postcentral gyrus
10	7.46	4.37	−6 2 10	L thalamus
11	6.34	4.03	18 0 14	R thalamus
Attention Left > Attention Right				
145	6.91	4.21	28 −98 18	R cuneus and middle occipital gyrus
Attention Right > Attention Left				
175	9.25	4.80	−22 −100 6	L cuneus and middle occipital gyrus
96	6.19	3.98	−28 −66 −12	L fusiform gyrus
40	5.87	3.87	16 −2 46	R cingulate gyrus
18	5.30	3.66	−40 −76 6	L middle occipital gyrus
15	5.03	3.55	−36 −80 −10	L inferior occipital gyrus

were the subject of primary investigation. The ROI center within each individual was determined by the local maximum ($p < .001$ and $p < .01$, for attention minus passive viewing and attention left vs. right, respectively) closest to peak coordinates from the corresponding group random effects analysis, in the appropriate anatomical landmark (Table 2). Anatomical definitions of each region were as follows: the anterior portion within the depth of IPS (e.g., Ikkai & Curtis, 2007; Kincade et al., 2005; Donner, Kettermann, Diesch, Villringer, & Brandt, 2003; Wojciulik & Kanwisher, 1999), the junction between the middle frontal gyrus and the precentral sulcus for FEF (e.g., Connolly, Goodale, Menon, & Munoz, 2002; Paus, 1996), and dMOG (e.g., Hopfinger, Woldorff, Fletcher, & Mangun, 2001).

The ROI center was located at the peak of activation nearest to the group coordinate within the appropriate anatomical region and included voxels within a sphere with a radius of 2 mm (see Figure 2; Tables 1 and 2). In

addition to identifying specific voxels, we extracted the time series from all voxels within each ROI using the eigenvariate tool in SPM 5. The time series was transformed into percent signal change by normalizing values by the baseline signal during blank fixation. Using coordinates from the group results as guides provided some uniformity between subjects and generality to the population, but locating the ROI center based on individual functional contrasts and anatomy resulted in greater precision. All ROIs were identified in both hemispheres, and where no differences arose between hemispheres, the data were collapsed.

RESULTS

Behavioral Response and Eye Position Analyses

Subjects were instructed to only attend to the stimulus in the cued visual field and report the orientation of

Table 2. Individual and Mean Coordinate Values for Regions of Interest

Subject	Anterior Intraparietal Sulcus		Frontal Eye Fields		Middle Occipital Gyrus	
	L x y z mm	*R x y z mm*	*L x y z mm*	*R x y z mm*	*L x y z mm*	*R x y z mm*
1	−26 −42 42	36 −42 42	−28 −6 50	30 −6 48	−30 −92 12	34 −88 18
2	−32 −48 40	40 −40 42	−38 −12 52	36 −10 48	−22 −90 8	− − −
3	−28 −46 42	38 −44 44	−38 −6 50	38 −4 64	−26 −92 6	32 −92 14
4	−30 −38 46	34 −44 48	−28 −10 60	38 −4 52	− − −	26 −90 10
5	−30 −50 44	40 −50 44	−32 −2 56	36 0 50	−26 −96 16	30 −92 24
6	−32 −52 56	32 −56 42	−26 −8 50	30 −8 54	−26 −98 16	22 −100 8
7	−42 −42 54	36 −32 40	−20 −10 58	28 0 56	−28 −98 2	22 −94 6
8	−28 −44 40	36 −44 42	−38 −8 48	32 −10 50	−24 −94 14	26 −92 2
9	−26 −46 52	34 −46 50	−28 −8 50	30 −2 48	−24 −94 6	34 −92 8
10	−30 −36 46	34 −32 42	−26 −6 48	36 −4 52	−18 −92 4	22 −90 10
11	−40 −36 38	38 −38 38	−28 −6 44	46 −2 48	−22 −92 8	24 −100 4
12	−40 −44 44	34 −42 40	−32 0 56	38 −4 48	−26 −98 6	22 −88 2
Mean	**−32 −44 45**	**36 −43 43**	**−30 −7 52**	**35 −5 52**	**−25 −94 9**	**27 −93 10**

lines whenever the ''mask'' was replaced with a target. On some trials, either the target in the attended location or the nontarget in the unattended location was perceptually salient (see Methods). Subjects were informed that perceptual salience was task-irrelevant and that they should instead always attend to the cued stimulus. The primary question in this experiment dealt with the effect of task-irrelevant perceptual salience on behavioral and brain responses to a voluntarily attended lateralized stimulus.
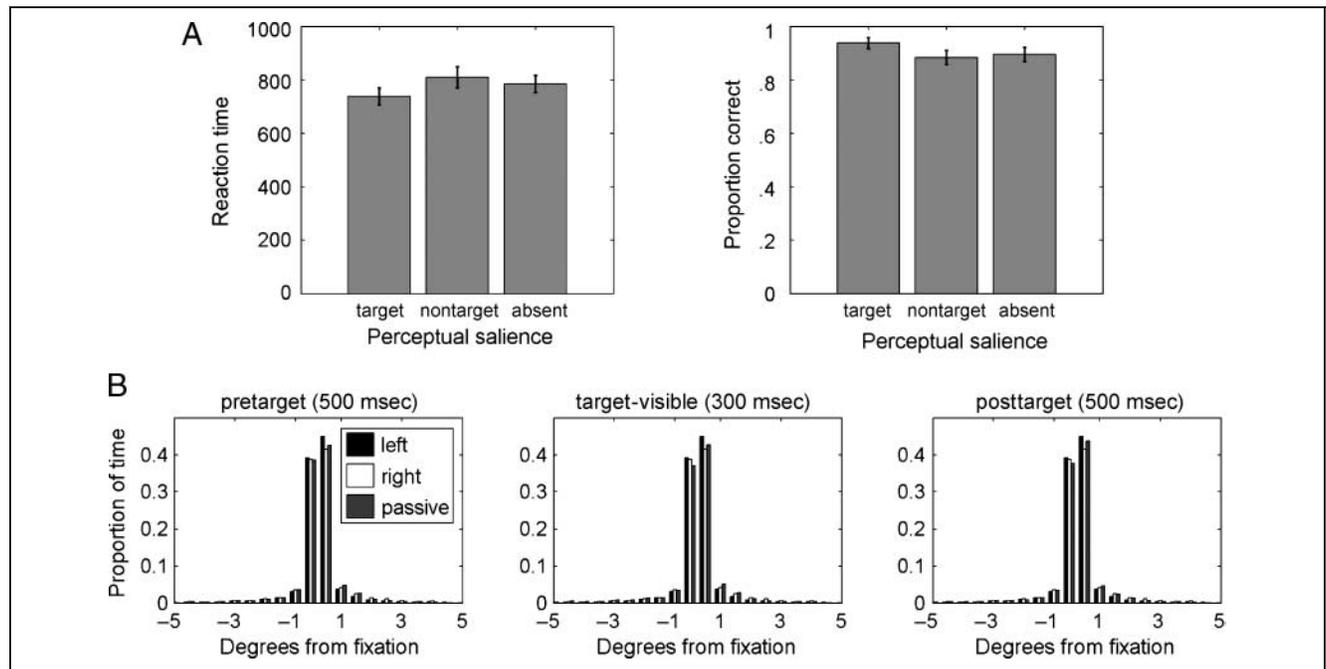

Figure 2. (A) Behavioral reaction time (RT; left) and accuracy (right) data showing a main effect of perceptual salience. Responses were significantly slower and less accurate when the nontarget was perceptually salient than all other conditions. (B) Eye position data showing the proportion of time spent at a distance from central fixation (in degrees of visual angle). The three cued spatial attention conditions of left, right, and passive are plotted in blue, red, and gray, respectively. The panels correspond to pretarget, target–target, and posttarget time epochs.

Behavioral data from the six conditions of main interest given by crossing spatial attention (left, right) and perceptual salience (attended target, unattended nontarget, absent) were entered into a repeated measures ANOVA, which resulted in only a significant main effect of perceptual salience [RT: $F(2, 22) = 20.3$, $p < .0001$, Figure 2A, left; Accuracy: $F(2, 22) = 5.4$, $p < .05$, Figure 2A, right]. Paired t tests demonstrated significant differences between all salience conditions in RT, and between salient attended targets and unattended nontargets in the accuracy data (Bonferroni corrected, $p < .05$). Salient nontargets interfered with responses, verifying that our experimental manipulation of salience was effective in capturing attention even when the location of the target was known in advance.

Eye position data were successfully collected from 10 subjects during the fMRI experiment. Data from correct trials that were also included in the fMRI analyses were analyzed. For each subject, eye position data from each of the three attentional cue conditions (left, right, passive) were divided into the following time epochs: a 500-msec "pretarget" period prior to the onset of the target and the nontarget, a 300-msec "target-visible" period during which the target and the nontarget were visible, and a 500-msec "posttarget" period following the reappearance of the mask stimuli. Histograms of

the proportion of time spent from central fixation in degrees of visual angle during each of attention condition and time epoch are plotted in Figure 2B. More than 87% of the time was spent within 1° of visual angle in each of the time epochs, indicating that subjects were able to maintain central fixation. Importantly, when the recorded eye position was outside of 1° (<13% of total), there were no differences between any attention conditions (left, right, passive) in time spent either to the left or right of fixation [i.e., eye positions were not skewed toward the attended side; all $t(9) < 1.2$, $p > .28$; see Figure 2B]. Subjects were able to perform the task without differences in eye position between the different conditions of spatial attention and, therefore, activations observed during imaging could not be a consequence of systematic differences in eye movements between conditions.

Cued Spatial Attention

In order to select functional coordinates for aIPS and FEF ROIs based on the general attentional demands of the task, we contrasted trials with lateralized attention with passive viewing (see Methods, Figure 3A, Table 1 for results from whole-brain analyses, and Table 2 for individual ROI coordinates). To determine if the attentional

Figure 3. Illustrations of selected ROIs. (A) Average center coordinates for aIPS and FEF ROIs (circled) selected from individuals based on group random effects analyses constrained by individual functional results and anatomy (see Methods). Underlying anatomy is the mean structural image from all subjects. (B) Time-series data plotted as the BOLD percent signal change from a blank fixation baseline.
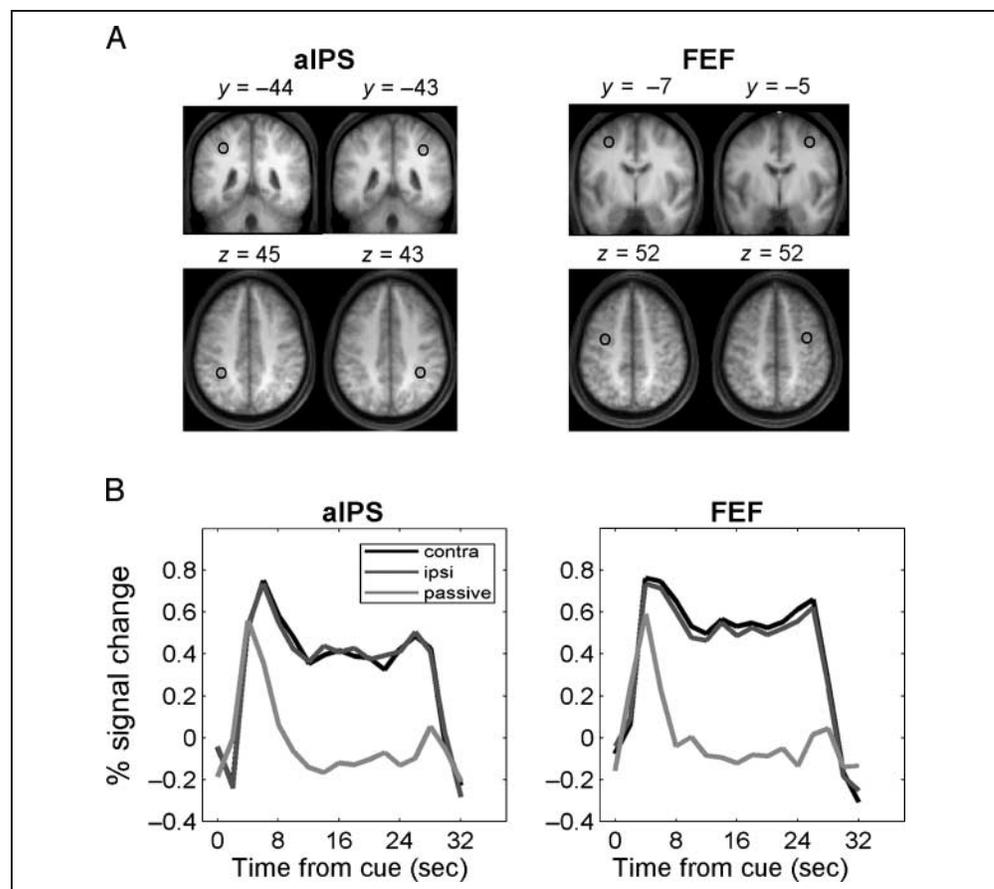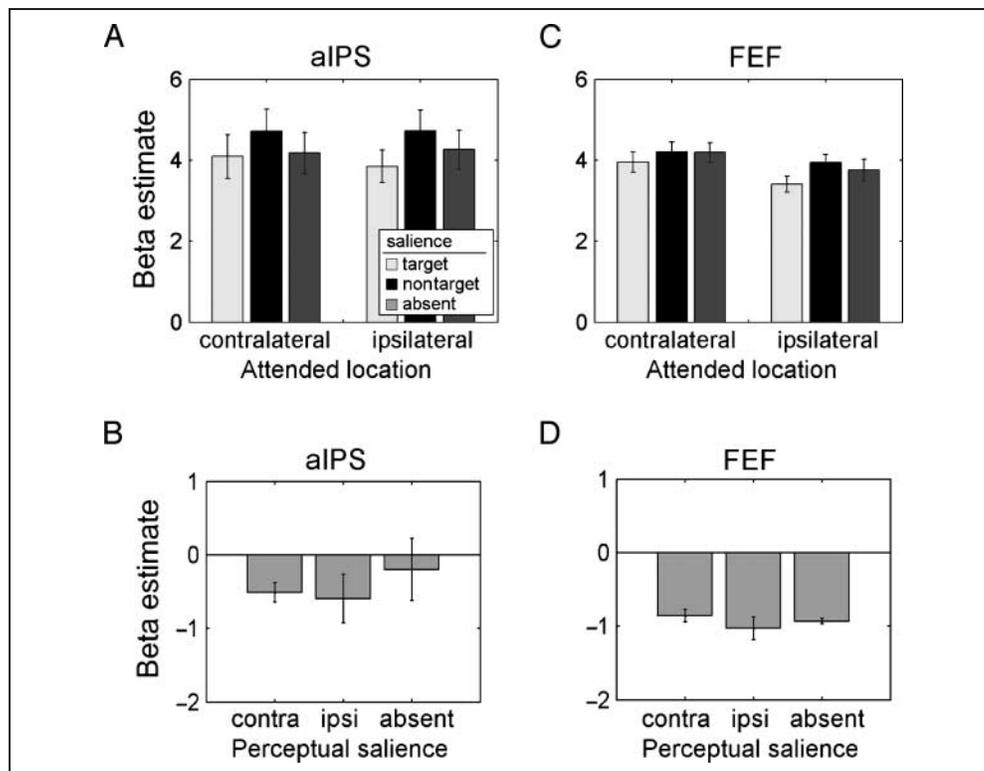
Figure 4. (A and C) aIPS and FEF beta parameter estimates from six attention conditions. Perceptually salient nontargets produced the largest responses irrespective of the attended location in aIPS. (B and D) aIPS and FEF beta estimates for each condition of perceptual salience during passive viewing.

modulations within aIPS and FEF depended on the duration of the attentional block, we examined the BOLD time series beginning from the first onset of the spatial cue (and masks; see Methods) until the end of the attentional block 24 sec later.

The results are plotted in Figure 3 and demonstrate that responses in aIPS and FEF were greater for both contralateral and ipsilateral attention than for passive viewing beginning 6 sec after the cue onset and lasting until 4 and 2 sec after the offset of the spatial cue at the end of the block, respectively [all $t(11) > 2.6$, $p < .05$ with Bonferroni correction; Figure 3B]. The apparent rapid return to baseline is likely due to subjects disengaging their attention from the task immediately after responding to the sixth and final target, which was still followed by an average interstimulus interval (ISI) of 4 sec. The substantial and sustained difference from passive viewing demonstrates that the responses in aIPS and FEF were not due to alerting or visual effects related to the onset of stimuli, but rather due to their involvement in establishing and maintaining task-related attentional control throughout the entire block. In addition to their similarities, FEF activation peaked slightly earlier at 4 sec after cue onset and aIPS activation peaked 6 sec after cue onset.

Effect of Perceptual Salience

Having established the presence of voluntary attentional responses in aIPS and FEF, we next tested for additional sensitivity in each ROI to the manipulation of task-irrelevant perceptual salience. Recall that salient nontargets captured attention away from the target, as indexed by slower and less accurate behavioral responses to the target when the nontarget was perceptually salient (see Figure 2A). A brain area that codes the attentional priority of objects based on both goal-directed and sensory-driven information should similarly have greatest activation in response to perceptually salient nontargets. In contrast, an area with a specific spatial representation of the target location, which would not change based on features of the unattended stimulus, should not be modulated by perceptual salience.

We compared for each ROI separately the conditions corresponding to attention (contralateral, ipsilateral) crossed with perceptual salience (attended target, unattended nontarget, absent) using repeated measures ANOVA. The two hemispheres (left, right) were also included to test for any differences between homologous ROIs from different hemispheres, but no significant differences involving hemisphere were found.

In aIPS only the main effect of perceptual salience was significant [$F(2, 22) = 4.2$, $p < .05$; Figure 4A]. Subsequent t tests showed that activation in aIPS was significantly greater when the unattended nontarget was perceptually salient than when the attended target was salient (Bonferroni corrected, $p < .05$). Activation in aIPS depended on whether salience was associated with the target or the nontarget, the two conditions that also produced the greatest differences

in behavioral response. The presence of the same perceptually salient stimuli produced no significant effects when subjects simply viewed them passively [$F(2, 22) =$ 0.8; Figure 4B]. This demonstrated that aIPS was sensitive to perceptual salience specifically as a function of the current location of spatial attention: Different responses to perceptual salience only occurred when attention was engaged at a cued location suggesting that this difference carried information about the distribution of attention rather than information about the perceptual qualities of the stimulus per se.

To further explore whether there were stronger effects when the nontarget was contralateral, we calculated a laterality index based on the ratio of beta estimates for salient nontargets to targets for each subject. Subjects with values greater than one showed the same effect as in the group data (see Figure 4A; see above). As shown in Figure 5A, more subjects had laterality indices greater than one when the salient nontarget was contralateral (and the target ipsilateral; 11/12 subjects) and fewer when the salient nontarget was ipsilateral (and the target contralateral; 7/12) (see Figure 5A; cf. aIPS pattern with FEF in which no such bias for nontarget salience was present). The stronger and more reliable effects in aIPS contralateral to the nontarget suggest weak speci-

ficity for the location of the salient nontarget (see Discussion), but the more general response in aIPS to the presence of sensory-driven perceptual salience as a function of the attended location was bilateral. Activity in aIPS mirrored that of behavior (see Figure 2) and suggests that aIPS represents the distribution of attention to objects present in the visual field such that greater activation in response to a salient nontarget corresponds with attentional capture by that nontarget (see section below).

In contrast to activation in aIPS, in FEF there were no significant effects of perceptual salience or interactions between perceptual salience and the attended location [all $F(1, 11) < 1.7$, $p > .21$]. Instead, FEF activation was greater overall during contralateral attention compared to ipsilateral attention [FEF: $F(1, 11) =$ 25.4, $p < .001$; Figure 4C]. Although small in magnitude, the effect was present in all subjects except for one, for whom the difference (0.06) was in the same direction (see Figure 5B; cf. aIPS). Similar to aIPS, however, there were also no significant differences between any of the perceptual salience conditions during passive viewing (Figure 4D), suggesting that FEF responded only during conditions of attention and additionally during contralateral attention.

Figure 5. Laterality indices. (A) Each symbol represents the beta ratio of salient nontargets and targets in one subject. Points above the diagonal indicate larger values for salient nontargets than targets. Circles (°) denote ipsilateral nontargets (contralateral targets) and stars (*) denote contralateral nontargets (ipsilateral targets). Salient contralateral nontargets produced more reliable effects across subjects in aIPS than ipsilateral nontargets (left), but a bias was present for both. No such bias was present in FEF (right). (B) Beta ratios for all contralateral and ipsilateral targets. There was no bias toward contralateral targets in aIPS (left), but a clear bias for greater activation in response to contralateral targets in FEF (right).
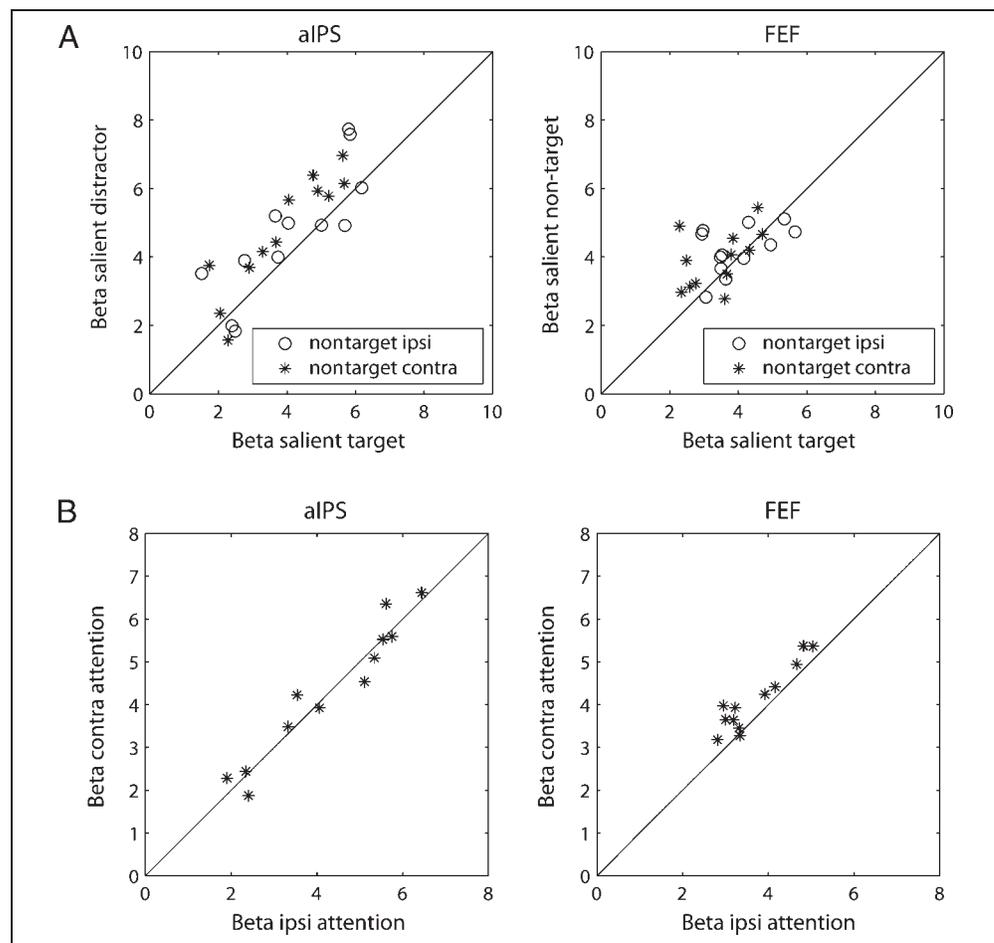
Although aIPS and FEF were engaged by voluntary spatial attention bilaterally, the finding of a difference between them in sensitivity to task-irrelevant perceptual salience and the location of spatial attention argues for separable roles in attentional control. aIPS activation integrated goal-directed and sensory-driven information and represented the attentional cost of capture by a perceptually salient nontarget, suggesting that aIPS codes the distribution of attention to objects in the visual field. In contrast, FEF activity was consistently greater when voluntary attention was directed toward the contralateral visual field, suggesting a stronger role in maintaining goal-directed spatial attention.

Correlation with Reaction Time

We next explored the functional significance of aIPS activation by examining the relationship between aIPS response amplitude and RT within individual salience conditions. Although our manipulation of salience was successful in altering patterns of behavioral performance overall, trial-by-trial variations in attentional focus prior to target onset should have also impacted the ability to select the target and filter out the nontarget stimulus. Thus, we would expect RT to be related to the strength of attentional focus on the cued target location prior to target onset (pretarget period) as well as the amount of attentional capture away from the target location once the target and nontarget appeared (target-evoked period). An area involved in pretarget attentional enhancement should be inversely related to RT and an area involved in representing nontarget attentional capture should increase monotonically with RT.

BOLD time series (in terms of % signal change from the fixation baseline) were extracted from FEF, aIPS, and dMOG ROIs. dMOG ROIs were defined by greater activation during contralateral compared to ipsilateral attention (Table 2; see Methods), and were expected to reflect the strength of attentional enhancement at the cued target location (Bestmann et al., 2007; Ruff et al., 2006; Weissman, Roberts, Visscher, & Woldorff, 2006; Moore & Armstrong, 2003). dMOG ROIs were located contralateral to the target stimulus. The group-average x y z MNI coordinates were the following: left = −25 −94 9 and right = 27 −93 10 (see Table 2; for similar coordinates in lateralized attention tasks, see also Hopf et al., 2006; Hopfinger et al., 2001).

For each salience condition (nontarget, target, and absent), data were divided into four bins based on each subject's RT distribution. Boarders between bins were defined by standard deviations from the mean ($< −1SD$, $−1SD$, $+1SD$, $> +1SD$) to account for the positive skew in RT distributions (Hockely, 1984; Ratcliff & Murdock, 1976; McCormack & Wright, 1964). An average of 15, 71, 39, and 20 trials occurred in each of the four bins, respectively. Data from one subject were incomplete and so were excluded from all time-series analyses.

Time-series data from each salience condition and ROI are plotted in Figure 6.

Consistent with the expectation that pretarget activation in contralateral target-occipital cortex should reflect the degree of attentional enhancement at the cued target location due to prior knowledge, Spearman's rank-order correlation between the response amplitude in dMOG (at 0 sec) and RT bin was significant for each salience condition (r_s: nontarget = −.37 $p < .05$, target = −.55 $p < .0001$, absent = −.42, $p < .005$; see Figure 7). Target-evoked activity was only significant in dMOG at 8 sec when the target was salient ($r_s = −.34$, $p < .05$). Significant correlations between dMOG activations and RT were not found during ipsilateral attention (r_s: nontarget = −.08, target = −.22, absent = −.05, all $p > .14$), indicating that the negative correlation was specific to areas of the visual cortex representing the target location. The negative correlations between target-contralateral dMOG and RT was significant for all salience conditions, but pretarget occipital activation explained the most variance in RT when the target was perceptually salient (r_s^2: nontarget = 13.7%, target = 30.2%, absent = 17.6%) and when sensory-driven salience *matched* the attended target location.

In contrast to pretarget activity in dMOG, the target-evoked activation in aIPS (at 6 and 8 sec) had a positive linear relationship with RT bin, (r_s at 6 sec: nontarget = .38, $p < .01$; target: = .41, $p < .05$; absent = .36, $p < .05$; r_s at 8 sec: nontarget = .66, $p < .0005$; target: = .43, $p < .005$; absent = .24 $p = .11$; see Figure 7). Pretarget activations (0 msec) were only significantly related to RT when the nontarget was salient ($r_s = −.33$, $p < .05$). Additionally, also in contrast to dMOG results, the target-evoked aIPS activation predicted RT best when the nontarget was salient (r_s^2: nontarget = 43.6%, target = 18.5%, absent = 13.0%), suggesting that nontarget attentional competition was more represented in aIPS.

To test whether the combined information from pretarget attentional enhancement and target-evoked responses would have a stronger correlation with RT, we took the difference between activation from the target-evoked aIPS time point with the highest correlation and pretarget dMOG values and calculated new correlation values with RT bin (r_s: nontarget = .67, $p < .0005$; target = .55, $p < .0005$; absent = .48, $p < .005$; Figure 7). These values were not substantially changed when activation in FEF was partialled out (r_s: nontarget = .61; target = .51; absent = .46); see Figure 6C, FEF activation plotted for comparison with aIPS. Interestingly, combining information from pretarget dMOG and target-evoked aIPS did not substantially increase Spearman's ρ for trials with salient targets, compared to dMOG alone, nor for trials with salient nontargets, compared to aIPS alone. This suggests that the strength of attentional focus on the cued location best predicted RT when the sensory-driven capture
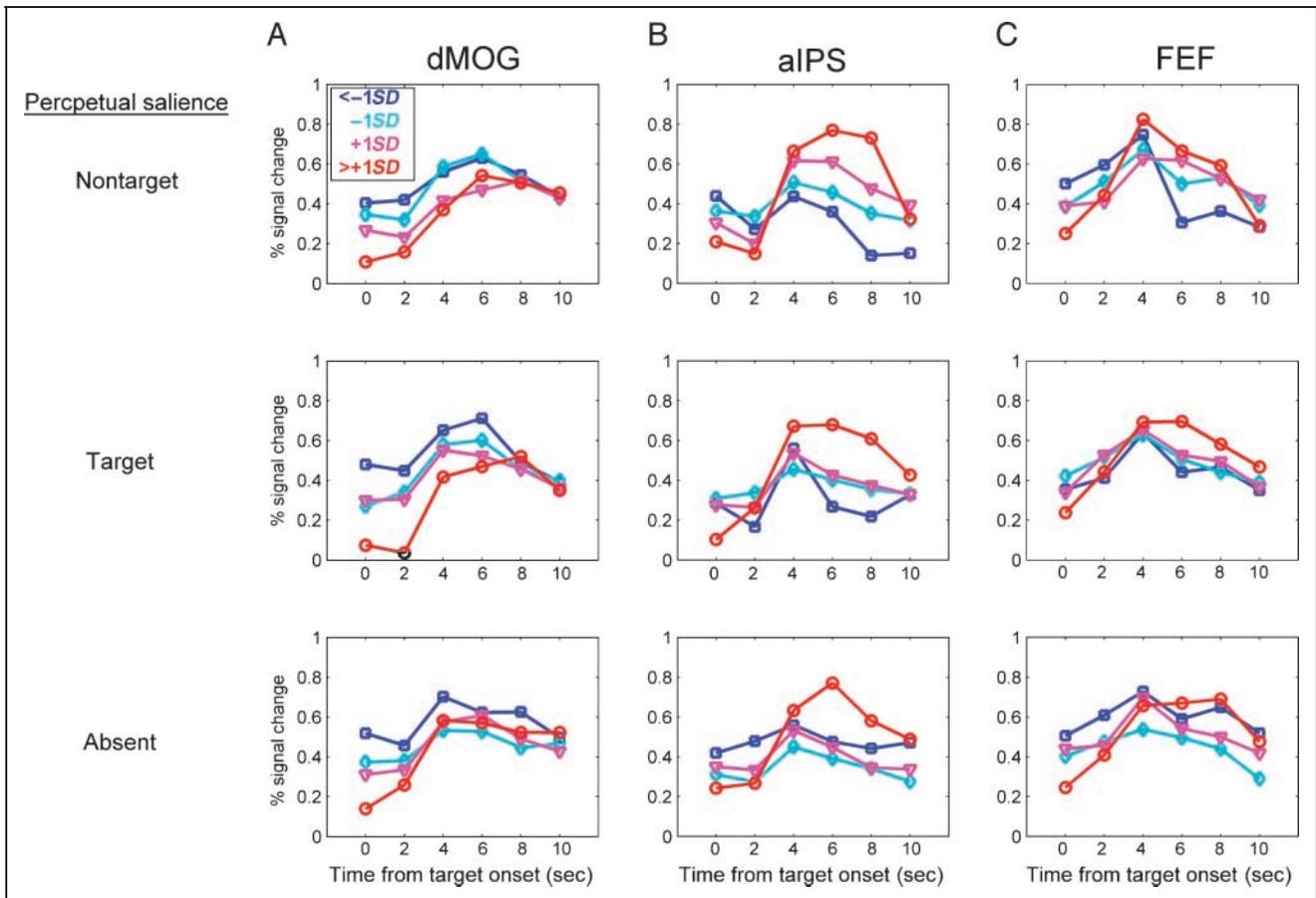
Figure 6. BOLD time series from trials in each salience condition binned by each subject's RT distribution (see Results). (A) Pretarget activation levels in dMOG correlated inversely with RT bin in all conditions and most so for target salience. (B) Target-evoked responses in aIPS had a positive linear relationship with RT in all conditions and most so during nontarget salience. (C) FEF time series are plotted for comparison.

by salience reinforced attention at the target location. However, when the nontarget was salient, the target-evoked response in aIPS explained the most variance, supporting the notion that aIPS activation reflected the degree to which attention was captured away from the cued target location.

Extra ROI Analyses

Although our question of interest primarily dealt with ROIs within the voluntary attention system, previous findings of the importance of the right TPJ (rTPJ) in detection of novel, or behaviorally relevant, stimuli (see

Figure 7. Spearman's rho correlation values between RT bin and BOLD response from the pretarget dMOG (black), the target-evoked aIPS (light gray), and combined information from the pretarget dMOG and the target-evoked aIPS (dark gray) in each of the three conditions of perceptual salience.
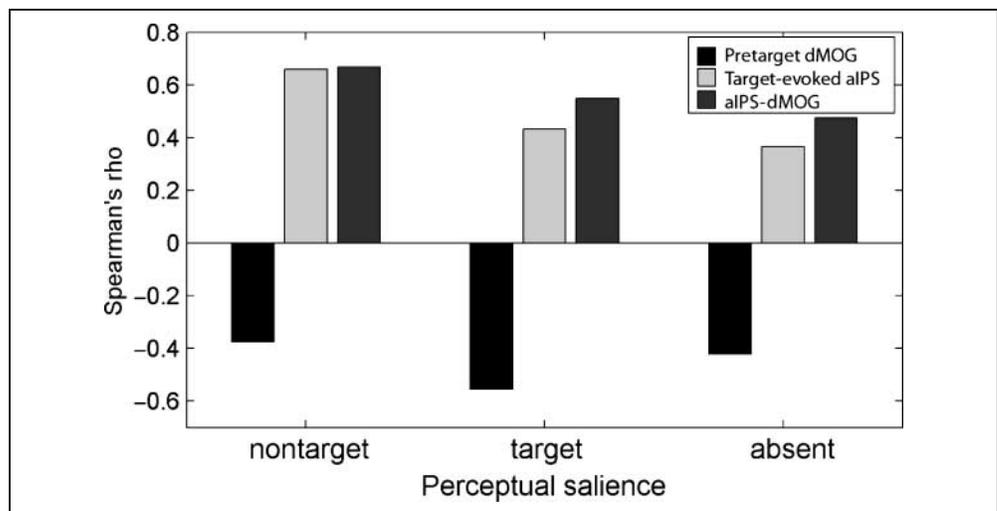
Introduction), compelled us to look at the rTPJ specifically for effects of nontarget salience. However, we did not see any significant pattern indicating that salient nontargets produced greater beta parameters than salient targets in either whole-brain analyses, or in individual ROIs based on coordinates of the rTPJ (e.g., from Downar et al., 2000; $x\ y\ z$ coordinates at 54 −42 13) and the right STG from Corbetta & Shulman (2002; $x\ y\ z$ coordinates at 57 −45 12). Transformation of Talairach coordinates to MNI was accomplished using a function by Matthew Brett (http://imaging.mrc-cbu.cam.ac.uk/imaging/ MniTalairach). Our null finding is consistent with the idea that attentional capture in rTPJ is subject to strong modulation by task relevance. In this task, the perceptually salient feature was completely task-irrelevant and the location of the target was known in advance. Thus, attenuating the response of a system that reorients attention makes good sense (e.g., see Corbetta et al., 2008).

In addition to TPJ, which was driven by hypotheses from the literature, we additionally looked in the whole brain for any areas that were specifically more activated in the presence of salient nontargets compared to salient targets. This contrast revealed three clusters of activation in the left and right ventral anterior cingulate (vACC) gyrus and left inferior frontal sulcus (see Table 3). aIPS activations in regions similar to those reported from the individual data (above) were found only at a lower statistical threshold (right aIPS group: $x\ y\ z$ = 32, −46, 46 significant at $p < .01$, uncorrected; left aIPS group: $x\ y\ z$ at −32 −50 50 significant at $p < .05$, uncorrected). This suggested that individual variability in our functionally and anatomically defined aIPS ROIs was substantial enough to mask observation of salience effects in group analyses. A priori selection of individually defined aIPS ROIs and analysis

Table 3. Whole Brain Results for Salient Nontarget > Salient Target

Cluster Size	t Score	Z Score	x y z mm	Region
27	7.26	4.31	−4 22 22	L ventral anterior cingulate
23	6.44	4.06	4 32 16	R ventral anterior cingulate
13	5.91	3.89	−40 16 24	L inferior frontal sulcus

of unsmoothed data were essential in uncovering sensitivity to perceptual salience as a function of the location of attention (see above).

The bilateral vACC are known to part of the "default network" (e.g., Greicius, Krasnow, Reiss, & Menon, 2003; Gusnard & Raichle, 2001; Raichle et al., 2001) and we similarly found that beta estimates were generally negative in our task, but conditions with a perceptually salient nontarget resulted in a relative reduction in deactivation (Figure 8A and B). This result is consistent with the notion that the default network is attenuated during goal-directed behaviors (e.g., Gusnard, Akbudak, Shulman, & Raichle, 2001) such as discrimination of a target object at a cued location and that a salient nontarget disrupted these task-related processes. The pattern in the inferior frontal sulcus suggests that this area was actively involved in task-related control to maintain attention on the target location when attentional competition was present (Figure 8C). However, despite the significantly greater activation for salient nontargets compared to salient targets, there were no systematic nor significant correlations between the target-evoked BOLD response in each salience condition and RT bin (r_s at 6 and 8 sec: nontarget = .18,
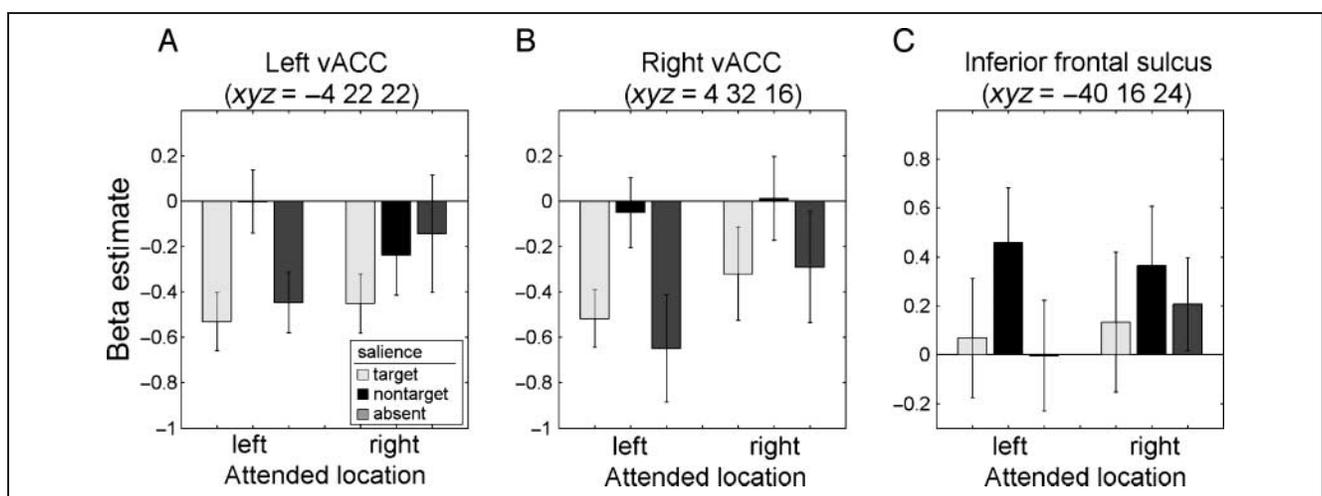

Figure 8. Beta estimates from areas with significantly greater activation in response to salient nontargets than targets, based on whole-brain group analyses. (A, B) The left and right vACC (part of the "default network"). (C) Inferior frontal sulcus activation related to cognitive control during trials with greater nontarget competition.

−.09; target = .24 −.15; nosal = .05, −.28). This suggested that this region was not related specifically to attentional orientation, but rather to other task demands associated with trials that were more or less difficult.

DISCUSSION

FEF and aIPS are areas that are commonly thought to be involved in controlling voluntary spatial attention by biasing processing in the visual cortex (e.g., Ruff et al., 2008; Sylvester et al., 2007; Silvanto et al., 2006; Moore & Armstrong, 2003; Corbetta et al., 2000; Hopfinger et al., 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999), but their respective roles in top–down versus bottom–up processes remain unclear. In the present study, we used a lateralized spatial attention task in which bilateral stimuli were presented and the location of the target was always known in advance. Subjects were required to make a perceptual judgment about the attended-location stimulus. On some trials, either the target in the attended location or the nontarget in the unattended location was perceptually salient. Perceptual salience was always task-irrelevant. This design enabled a conservative test of sensory-driven attentional selection because there was no reason to voluntarily attend to the stimulus in the nontarget location. Nevertheless, the behavioral data demonstrated that our manipulation of perceptual salience captured visual attention: Performance was slower and less accurate when the nontarget was salient compared to the target (see Figure 2).

Sustained BOLD activations were present in FEF and aIPS in both hemispheres over the entire duration of the attentional block (e.g., Fan et al., 2007; Ikkai & Curtis, 2007; Kelley et al., 2007; Serences & Yantis, 2007; Silver, Ress, & Heeger, 2005, 2007; Moore & Armstrong, 2003; Yantis et al., 2002; Vandenberghe et al., 2000), confirming that both ROIs were actively involved in maintaining goal-directed spatial attention. In addition to general effects of spatial attention, however, only FEF had greater activity during attention to the contralateral visual field. The contralateral bias suggested that FEF was involved in maintenance of goal-directed spatial attention, which would be consistent with literature showing that FEF activation plays a causal role in biasing activity in the visual cortex, and enhancing perceptual sensitivity in corresponding regions of the visual field (e.g., Ruff et al., 2006, 2008; Armstrong et al., 2006; Chambers et al., 2006; Mevorach et al., 2006; Muggleton et al., 2006; Silvanto et al., 2006; Hung et al., 2005; O'Shea et al., 2004; Moore & Armstrong, 2003; Grosbras & Paus, 2002). Greater pretarget activation in the target-contralateral dMOG presumably leads to higher quality representations of the target stimulus when it appears and, therefore, faster RTs (Weissman et al., 2006). Consistent with this, we found that pretarget activation in the target-contralateral (but not target-ipsilateral) dMOG

was inversely related to RT in all salience conditions, but more so when the salient stimulus was the target; pretarget occipital activations had the highest correlation with RT when nontarget competition for attention was the lowest (i.e., when only the target was salient; see Figures 6 and 7).

In contrast to FEF, aIPS showed no contralateral bias in activation as a function of target location. Instead, aIPS activation was greatest when the unattended (nontarget) stimulus was perceptually salient. Target-evoked activations in aIPS also correlated positively with RT in all conditions, but was highest when the nontarget was salient. Greater target-evoked aIPS activations occurred on trials with slower RTs and this was opposite to the pretarget effects found in dMOG (described above; see Figures 6 and 7), suggesting that aIPS reflected the degree to which attention was directed away from the target stimulus. This result argues against the idea that bigger aIPS activation could represent greater attentional suppression of the nontarget. If greater activation meant greater suppression, then higher amplitude responses should have lead to faster RTs, not slower.

Another possibility is that aIPS is involved in holding items in visual short-term memory (e.g., Xu, 2007) and trials with greater activation reflected the storage of both the target and nontarget objects in memory. However, the linear relationship between aIPS response amplitudes and RT (even within conditions with identical stimuli) argues against the categorical storage of object items in this study. If aIPS activation reflected the storage of a discrete number of objects, then we would expect only two response levels based on whether one or two items were stored. Instead, it seems that activation in aIPS reflected the distribution of attention, which can be understood in different ways: one is that it reflects a shift of attention of varying durations (or engage and disengage operations; e.g., Posner, Walker, Friedrich, & Rafal, 1984; Posner, Cohen, & Rafal, 1982) to the nontarget and then to the target on trials when attention was captured by the salient nontarget. Alternatively, the distribution of attention could represent an attentional priority map that codes the relative strength of competition for attention by all stimuli in the visual field (e.g., Gottlieb, 2007; Goldberg et al., 2006; Itti & Koch, 2000). Here, greater activation (e.g., in response to trials with a salient nontarget) would reflect the presence of more items with higher attentional priority, even if attention is ultimately only shifted to the "winner" with the highest relative priority (e.g., Bisley & Goldberg, 2003). It is not possible to know from the current data whether attention was actually shifted to the nontarget because we did not explicitly measure behavioral performance at the nontarget location. However, the response in aIPS clearly contained a graded representation of the state of competition for attention under all conditions of perceptual salience and this suggests that aIPS represents the state of attention, rather than stimulus salience per se

(although stimulus salience obviously had a strong affect on the state of attention).

An unexpected aspect of our aIPS results was the lack of stronger hemispheric lateralization based on the attended visual field. Although aIPS contralateral to the nontarget did produce more robust results, it perhaps seems surprising that the results were not more lateralized given recent reports of topographically organized attentional maps in the human IPS as well as FEF (e.g., Saygin & Sereno, 2008; Kastner et al., 2007; Swisher, Halko, Merabet, McMains, & Somers, 2007; Schluppeck, Curtis, Glimcher, & Heeger, 2006; Silver et al., 2005; Sereno, McDonald, & Allman, 1994). However, it is worth noting that data from studies that used cognitive tasks rather than specific mapping procedures have often found strong bilateral effects in both IPS and FEF, which only sometimes also contained weaker contralateral sensitivity (e.g., Curtis & Connolly, 2008; Ikkai & Curtis, 2007; Indovina & Macaluso, 2007; Kelley et al., 2007; Serences & Yantis, 2007; Geng et al., 2006; Kincade et al., 2005; Donner et al., 2002; Hopfinger et al., 2000; Wojciulik & Kanwisher, 1999). In addition, areas with retinotopic attentional maps in IPS such as IPS1 and IPS2 (Silver et al., 2005), and IPS3 and IPS4 (Swisher et al., 2007), tend to be more posterior than IPS regions that show bilateral attentional effects (see above), including our current findings. It is unclear whether discrepancies in topographic specificity arise due to meaningful functional differences between subareas within IPS, or due to experimental design factors (e.g., stimulus eccentricity), and requires further investigation. Nevertheless, it is clear that regions within FEF and IPS in both hemispheres are critically involved in the control of sustained voluntary spatial attention (e.g., Fan et al., 2007; Ikkai & Curtis, 2007; Serences & Yantis, 2007; Silver et al., 2005; Yantis et al., 2002; Vandenberghe et al., 2000) and this study extends those findings by demonstrating differences in function between these areas such that only aIPS was sensitive to salience of stimuli as a function of the location of attention.

Our results that show sensitivity in aIPS to task-irrelevant perceptual salience may initially seem at odds with reports that salient stimuli that are completely task unrelated are not represented in attentional control regions, or even early visual areas (e.g., Beck & Kastner, 2005; Schwartz et al., 2005). Those studies differed from ours, in that subjects were required to engage in a task at central vision and the task-irrelevant salient stimuli appeared in the periphery. It may be that peripheral salient stimuli can be effectively inhibited when attention is concentrated centrally or when they occur during periods when task stimuli are absent (Indovina & Macaluso, 2007). In line with this, we also found that neither aIPS nor FEF responded significantly to the presence of the salient stimuli during passive viewing when no attentional task was required (although we did find greater activation to perceptually salient stimuli in dMOG

ROIs). This suggests that our result in aIPS of perceptual salience was a function of the attended location: aIPS activation reflected the degree to which a perceptually salient nontarget captured attention away from the target and argues for a model of attention in which voluntary and stimulus-driven properties are represented within the same areas that control covert and overt selection.

We additionally examined areas outside of our ROIs using whole-brain voxelwise analyses to test for other regions that might also show sensitivity to salient nontargets as a function of attention. In the rTPJ, an area hypothesized to be involved in sensory-driven attentional reorienting, we found no effects of nontarget salience. This result is consistent with the rTPJ being involved with attentional orienting specifically toward goal-relevant stimuli that may also violate expectations (e.g., Vossel, Weidner, Thiel, & Fink, 2009; Corbetta et al., 2008; Kincade et al., 2005; Downar et al., 2000), and not stimulus-driven attentional capture by irrelevant features of behavioral nontargets. We also found a reduction in negative activation for salient nontargets in the ACC bilaterally. The ACC is considered part of the "default network" (e.g., Greicius, Supekar, Menon, & Dougherty, 2008; Raichle et al., 2001), suggesting that the presence of salient nontargets required greater task engagement. There was also greater activation for salient nontargets in the inferior frontal sulcus, but we did not find any parametric relationship between activation in the inferior frontal sulcus and RT, suggesting that the role was not in attentional control per se, but rather in executive functions related to staying on task.

In summary, we examined FEF and aIPS in a sustained attention task when the perceptual salience of stimuli varied randomly. Although both regions were involved with selective spatial attention in general, we observed differences in the representation of attended spatial locations and perceptual salience within FEF and aIPS. FEF activation was biased by the location of spatial attention, whereas aIPS was modulated by the relative perceptual salience of the target and nontarget stimuli. The target-evoked response in aIPS scaled linearly with increasing RT in all conditions, but especially when the nontarget was salient. aIPS was most correlated with RT when attention was captured by the salient nontarget, suggesting that aIPS responses are sensitive to task-irrelevant perceptual salience within the context of goal-directed spatial attention. Despite strong bidirectional anatomical and functional connections between FEF and IPS (e.g., Pesaran, Nelson, & Andersen, 2008; Buschman & Miller, 2007; Ferraina, Pare, & Wurtz, 2002; Blatt, Andersen, & Stoner, 1990), these results demonstrate separable roles for FEF and aIPS in attentional control, with FEF more involved in goal-directed spatial attention and aIPS relatively more sensitive to bottom–up attentional influences driven by stimulus salience.

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